



RESEARCH PAPER

Win, Lose, or Draw: Effects of Residency, Size, Sex, and Kinship on High-Stakes Larval Contests in a Moth

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Abstract

Many factors can affect the outcome of a competitive interaction. One such factor is the relatedness between competitors as competitive intensity may decrease between kin. Because adult females lay eggs in clusters, larvae of the moth *Utetheisa ornatrix* are likely to be found in high densities of their siblings. Larval *U. ornatrix* actively compete for access into seedpods of their host plant (*Crotalaria* spp.), and successful competitors will reap numerous reproductive benefits during adulthood. The objective of this study was to determine whether residency, size, sex, and relatedness affect competition over seedpods in *U. ornatrix* larvae. In one-on-one trials for access into artificial seedpods, we monitored occupancy and weight change of larvae varying in residency, size, sex, and relatedness. We found that larger larvae have a competitive advantage over smaller larvae. This finding has consequences for the mating system of *U. ornatrix* in that females, by selecting males based on pheromone levels that are correlated with body size, can rear larger offspring that will have an advantage in competition over seedpods. These data did not support our hypothesis that males would outcompete females, perhaps because the rewards of acquiring a seedpod are substantial for both sexes. Finally, our data show that resident larvae are more likely to maintain control of seedpods over sibling than non-siblings intruders, which suggests that relatedness affects competitive interactions.

Introduction

Intraspecific competitive interactions are particularly prevalent because conspecifics are generally competing over the same resources. A multitude of factors can affect the outcome of a competitive interaction such as the competitor's status as either resource holder (resident) or intruder (Davies 1978; Morrell & Kokko 2003), the sex of the competitors (Leturque & Rousset 2004; Vergara & Fargallo 2008), and body size (Smith & Brown 1986; Iyengar & Starks 2008). Relatedness between competitors can also affect competition as competitive intensity often decreases between closely related kin (Reeve et al. 2000; West et al. 2001). Differential behavior based on relatedness has been well documented in competition over reproduction (e.g., Reeve et al. 2000), but competitive interaction over food can also be influenced by kinship (e.g., Pfennig et al. 1993).

Females of some insect species, including most Lepidopterans, lay eggs in clusters, rather than singly, resulting in local aggregations of siblings that will likely compete with both kin and non-kin (Stamp 1980). Benefits of egg clusters include an enhanced aposematic signal (Stamp 1980; Dimarco & Fordyce 2013), joint defense against parasitoids and parasites (Stamp 1980; Faraji et al. 2002), protection from desiccation (Clark & Faeth 1998), and increased efficiency of resource use (Tsubaki & Shiotsu 1982; le Masurier 1994). In assessing the benefits of laying eggs in clusters, one must tease apart the benefits of being in a group in general vs. the benefits derived from being around related individuals. Given that larvae may be competing with individuals of varying relatedness, it is possible that, given kin recognition mechanisms observed in insects (e.g., De Nardin & de Araujo 2011), there may be selection to decrease competition among siblings, either through domination of

the alpha/resident or decreased aggression of the beta/intruder (Johnstone 2008).

The rattlebox moth *Utetheisa ornatix* (Family Arctiidae) is a well-suited organism for studying competition because larval competition for food has consequences not only for survival, but also for eventual reproductive success (Iyengar & Eisner 1999b). Competition for access into seedpods is very intense due to high densities of larvae resulting from adult female *U. ornatix* laying clusters of 10–40 synchronously hatching eggs (Conner et al. 1990). *Utetheisa ornatix* is protected from most predators at all life stages by toxic pyrrolizidine alkaloids (PAs) and advertises its distastefulness through the use of aposematic coloration (Dussourd et al. 1988). PAs are sequestered as larvae from the host plants, *Crotalaria spectabilis* or *Crotalaria mucronata*, by consumption of the PA-rich seeds or leaves (Conner et al. 1981). The larvae of *U. ornatix* will often burrow into the seedpods of their host plant and remain in the seedpod while feeding on the seeds. Larvae have been observed competing for access into seedpods in nature by biting and chasing each other out of seedpods (pers. obs.). Although larvae will sometimes feed on the leaves of *Crotalaria* spp., larvae that succeed in acquiring a seedpod benefit from faster development, increased adult size, and a higher survival rate because seeds contain more defensive PAs and more nutrients than leaves (del Campo et al. 2005; Ferro et al. 2006). Additionally, although protected from most predators by PAs, *U. ornatix* larvae are vulnerable to parasitoids such as the tachinid fly *Archytas aterrimus* (Iyengar et al. 1999), and seedpods likely offer protection for larvae (Ferro et al. 2006).

Larval competition for PAs is especially crucial for the eventual reproductive success of *U. ornatix* males because they derive their main sex pheromone, hydroxydanaidal (HD), from the PAs they acquire as larvae (Conner et al. 1981). Furthermore, the amount of HD males produce is proportional to amount of PAs sequestered as larvae (Dussourd et al. 1991), and females use male HD levels as the main criterion of mate choice (Iyengar et al. 2001). Female moths are able to detect variations in HD levels and preferentially mate with males who have high levels of HD. Additionally, HD levels are proportional to male body size (Conner et al. 1990). Therefore, the HD levels of a male provide the female with the ability to assess his quality. Females gain both multiple benefits from choosing males based on HD levels, as choosy females receive more defensive chemicals (PAs) to bestow to her eggs (Dussourd et al. 1988), additional nutrients to increase her fecundity (LaMunyon 1997), and

genes encoding for the larger offspring (Iyengar & Eisner 1999a). Despite losing some PA through spermatophores transferred to the female, male HD titer remains constant even after multiple matings and is therefore an indicator of male quality (Kelly et al. 2012). Overall, larval competition for access into seedpods is crucial to both the survival and reproductive success of *U. ornatix*.

The importance of larval *U. ornatix* competition for seedpods raises interesting questions about which, if any, factors affect the competition outcome and whether larvae alter their behaviors based on the relatedness to their adversary. To that end, we devised a series of experiments to examine whether residency, body size, sex, or relatedness affect larval competition. We hypothesized that larger larvae would dominate smaller larvae because their larger body size and larger mandibles would allow them to physically exclude smaller larvae from seedpods. Additionally, we hypothesized that male larvae would outcompete female larvae because male competitive ability for PAs as larvae affects eventual reproductive success as adults. Also, female larvae can acquire additional PAs as adults through the nuptial gifts provided by males (Rossini et al. 2001), while males cannot acquire more PAs after metamorphosis. Finally, we predicted that competition would be more intense between unrelated larvae than between siblings. Therefore, we hypothesized that *U. ornatix* larvae would behave differently when competing with siblings instead of non-siblings, possibly by either sharing seedpods with siblings or being less likely to invade sibling residents. To test these hypotheses, we conducted resident vs. intruder competition trials for artificial seedpods.

Methods

Study Organism

All *U. ornatix* used in this study came from a laboratory-reared colony derived from 200 adult moths collected in May 2013 at Archbold Biological Station at Lake Placid, Florida. The colony was replenished with 40 additional adults in Dec. 2013. We established unique family lines of full siblings by isolating pairs of adult males and females in mating canisters and keeping track of their offspring. Before using larvae in a trial, we maintained all eggs from each female on a pinto bean diet in a single container for 2 wk before separating them into containers of 15–20 larvae. All larvae were reared for an additional 2 wk before use in trials, at which time competing individuals were selected from different containers. After use in trials,

all larvae were reared to pupation in isolation (approximately two additional weeks) and then frozen.

Resident–Intruder Staged Contests

We set up one-on-one competition trials in 85-mm-diameter plastic containers. All trials were conducted between Aug. 2013 and Mar. 2014. In each container, we placed a 42-mm-long clear plastic tube with a 10-mm-diameter opening to mimic a *C. spectabilis* seedpod. In each tube, we placed five *C. spectabilis* seeds and, to ensure that the seeds will not fall out due to the motions of the larvae, we taped a hole-punched circle of paper over the opening of the tube. Additionally, we broke open seeds and rubbed them over the outside of the tube, which resulted in larvae more easily finding the tubes. We did not use larvae in trials until they were at least 45 mg because our observations indicated that larvae are most vulnerable to dying within the first 2 wk, and we never used larvae over 200 mg because such larvae are near pupation and thus at risk of not feeding. Each larva was used in a trial only once to ensure independence (Hurlbert 1984).

We placed a larva (the ‘resident’) inside the artificial seedpod and gave it 1 h to become acclimated to the tube before introducing an intruder larva directly outside of the artificial seedpod. We allowed a larva to establish residency, rather than simultaneously releasing two larvae, because this is more similar to a natural setting as two larvae are unlikely to arrive concurrently at an unoccupied seedpod. Also, releasing two larvae simultaneously would essentially result in an identical scenario as one larva would most likely find its way into the tube first. We placed a dot of colored, non-toxic paint on the back of each larva to identify individuals during competition trials.

The two competing larvae also varied according to relative size, relatedness, and sex. We considered larvae to be ‘size-matched’ if their body masses were within 5% of each other and ‘different sized’ if their body masses were >10% different, as in previous studies (Iyengar et al. 2001). To test the effects of relatedness on competition, we set up trials such that the resident and intruder larvae were either full siblings or unrelated. We randomly assigned larvae into 1 of 12 trials (resident/intruder \times sibling/unrelated \times larger/size-matched/smaller). Although we also examined sex differences between the larvae, we could not consider sex during the trials because it is not possible to determine the sex of *U. ornatrix* larvae until after they molt into pupae. After use in trials, however, we fed the larvae in isolation through pupation, at which time we recorded their sex.

Each trial lasted 24 h. We weighed larvae both before and after each trial to determine their change in weight over the 24-h period and calculated the percent change in body weight for each larva. We determined who won (which larva was in the tube after the 24-h period) which resulted in four possible outcomes: resident won, resident lost, the two larvae shared the tube, or neither larva was in the tube.

To verify that larvae were not moving in and out of the seedpod arbitrarily and instead were actively competing for occupation of the seedpod, we utilized the location of larval frass to estimate the amount of seedpod occupation changes. Larvae that ate the pinto bean-based diet used to rear larvae in laboratory produce frass that is light brown in color. On the other hand, larvae that ate *C. spectabilis* seeds produce black frass. Therefore, we recorded the location of black frass in each trial to determine the position of larvae throughout the trial. For example, if black frass was found both inside and outside of the seedpod, we knew that a larva that was in the seedpod and feeding on the seeds spent some time outside of the seedpod. However, if the resident won the trial and black frass was found only in the seedpod, we could reasonably conclude that the resident likely spent the entire 24 h inside the seedpod.

Statistical Analyses

We analyzed the data using a logistic regression for binomial data (Quinn & Keough 2002) with winning or losing (i.e., found inside or outside the seedpod) as the dependent variable. We analyzed the percent change in weight data using a generalized linear model. In both models, we included the effects of residency, relative size, sex, relatedness, and all possible interaction terms. We also performed a chi-squared test of independence on the location of black frass. We performed all analyses in JMP Pro 11.

Results

Seedpod Winners

Overall, we used 146 trials in the analyses, the results of which are shown in Table 1. In our analyses of winners and losers, we disregarded trials in which neither larva was in the tube and we did not include any trials in which at least one larva died before reaching pupation, as these individuals were unable to be sexed. Additionally, as larvae shared the seedpod in only approximately 7% (17 of 222; 10 between non-siblings, seven between siblings) of the total trials, we did not include ‘draws’ in our data analyses.

Source	df	Winner χ^2	Winner p value	Weight change χ^2	Weight change p value
Residency	1	9.95	0.002	6.60	0.010
Relative Size	2	38.58	<0.001	6.14	0.046
Sex	1	~0	0.997	0.19	0.67
Relatedness	1	~0	0.997	5.07	0.024
Residency \times relative size	2	0.98	0.611	0.06	0.97
Residency \times sex	1	1.77	0.184	0.39	0.531
Residency \times relatedness	1	7.98	0.0047	7.42	0.007
Relative size \times sex	2	2.15	0.341	0.14	0.931
Relative size \times relatedness	2	0.72	0.698	0.02	0.992
Sex \times relatedness	1	~0	0.999	2.32	0.128
Residency \times relative size \times sex	2	2.55	0.279	1.25	0.534
Residency \times relative size \times relatedness	2	0.05	0.977	5.09	0.079
Residency \times sex \times relatedness	1	1.09	0.295	0.20	0.657
Relative size \times sex \times relatedness	2	0.16	0.921	0.194	0.907
Residency \times relative size \times sex \times relatedness	2	1.94	0.38	0.52	0.770

Significant effects are highlighted in bold.

We found a significant effect of relative size, as larger individuals outcompeted smaller ones in 78% (59 of 76) of the trials among different-sized individuals. Although we did find a significant effect of residency (overall, residents won 58% of the time), this pattern was driven by a significant interaction between residency and relatedness—residents won 68% (39 of 57) of the trials against a sibling but only 48% (43 of 89) of the trials when facing an unrelated opponent.

Change in Weight

Individuals that won their trial gained an average of $7.66 \pm 0.89\%$ (mean \pm SEM) of their body weight, while losers lost an average of $6.91 \pm 0.67\%$ of their body weight. We found a significant effect of relative size, as larger larvae gained an average of $3.30 \pm 1.04\%$ of their body weight, while smaller larvae lost an average of $2.08 \pm 1.14\%$ of their body weight (Table 1). Although we found significant effects of both residency and relatedness, we again found a significant interaction between residency and relatedness. In non-sibling trials, intruders gained $1.92 \pm 1.34\%$ while residents gained $1.36 \pm 1.40\%$ of their body weight. However, in sibling trials, residents gained $3.26 \pm 1.08\%$, while intruders lost $6.45 \pm 1.51\%$ of their body weight.

Black Frass

We recorded and analyzed the location of frass from all trials, regardless of the outcome or if larvae died before pupation ($n = 175$). The location of black frass

Table 1: Results of the GLMs on both the winner of the seedpod (winner) and the percent change in weight (weight change) based on residency, relatedness, relative size, and sex

was not independent of trial outcome ($\chi^2 = 71.54$, $df = 2$, $p < 0.001$). Residents won 79% (55 of 70) of the trials in which black frass was only found inside the seedpod but only 17% (18 of 105) of the trials in which black frass was found both inside and outside the seedpod.

Discussion

Our goal was to determine the effects of residency, size, sex, and relatedness on competitive interactions among *U. ornatrix* larvae. Given that larval feeding and weight gain ultimately affect adult body weight, caterpillars benefited from successfully controlling the seedpod in that they gained weight while losers suffered weight loss. The observed weight changes between winners and losers accrued during the larval stage may have substantial consequences on fitness as an adult, as it has been shown that a 10% difference in adult body weight corresponds to a difference of 30% in the number of grandchildren based on fitness consequences (Iyengar & Eisner 1999b). This loss in body weight is likely to delay the larval period (when individuals are non-reproductive and vulnerable to predators) or result in smaller adults. Losers likely lost weight because of a lack of food and increased movement while searching for food.

The patterns of black frass provided indications about the location of the larvae during the trials. In over 75% of trials won by the resident, we only found black frass inside the seedpod. This indicated not only that the resident likely never left the seedpod but also that the intruder was never able to feed on the seeds.

Additionally, trials won by the resident in which black frass was found both in and out of the seedpod do not necessarily indicate switches in larval control of the seedpod as larvae would sometimes be feeding on the seeds with their posterior end outside of the seedpod.

We did not find an effect of larval sex on competition for access into seedpods or on percent change in weight. We predicted that male larvae would outcompete female larvae because the amount of PAs acquired by male larvae is proportional to the amount of HD produced by males as adults and females preferentially mate with males based on HD levels. However, acquiring a seedpod is also crucial for females because all larvae benefit from faster development, increased adult size, and a higher survival rate when feeding on seeds rich in defensive PAs and nutrients (Ferro et al. 2006). Therefore, as both males and females may suffer severe fitness consequences if they fail to secure a seedpod, this may explain the lack of competitive differences based on sex.

The results did support our hypothesis that larger larvae would be better competitors than smaller larvae. Both residents and intruders were more likely to prevail in competitive interactions when they were larger than their opponent, as observed in many taxa (Andersson 1994). As larger larvae have an advantage over smaller larvae, competition should select for larger, faster developing larvae. Interestingly, PAs are phagostimulants; as a result, larvae that are successful at securing a seedpod and the PA-rich seeds inside will eat more and develop faster and become larger adults with fitness advantages (Iyengar & Eisner 1999b) than larvae forced to feed on the leaves (del Campo et al. 2005). Therefore, larvae that succeed in acquiring a seedpod initially are likely to maintain control of the seedpod over the slower developing larvae outside.

The finding that larger larvae dominate smaller larvae helps explain why females selectively mate with large males. As mentioned earlier, adult *U. ornatrix* females preferentially mate with males with high levels of HD (Iyengar et al. 2001) and HD levels are correlated positively with male body size (Conner et al. 1990). Because body size is heritable (Iyengar & Eisner 1999a), females, by choosing males based on HD levels, are selecting for larger offspring. Larger offspring are likely to succeed in acquiring a seedpod to feed on the PA-rich seeds which will stimulate them to develop faster and reach larger adult sizes (Ferro et al. 2006). Overall, larval competitive ability based on size is potentially a strong driving force in the *U. ornatrix* mating system.

There was an effect of the interaction of residency and relatedness, which supported our hypothesis that

larvae would behave differently when competing with full siblings, a pattern observed in other species where individuals compete over reproduction (Reeve et al. 2000; West et al. 2001). Residents were more likely to maintain control of the seedpod and gained weight relative to intruders when facing siblings as opposed to non-siblings. This could be the result of increased aggression by residents or decreased aggression of intruders when facing related competitors. Interestingly, individuals in non-siblings trials gained more weight than individuals in sibling trials. This result was driven by the fact that in sibling trials, the resident generally gained weight while the intruder lost weight. However, in non-sibling trials, the change in weight was more evenly distributed, often with both participants gaining some weight. Overall, our results suggest that larvae do compete differently based on the relatedness to their opponent and that competition within local aggregations of siblings may not be as intense as competition between unrelated larvae. As a result, *U. ornatrix* females may gain a fitness advantage by laying eggs in clusters as their numerous offspring will compete harder against non-kin while allowing siblings to maintain control of a seedpod.

Finding an effect of larval relatedness was surprising because previous work demonstrated that larval *U. ornatrix* were not able to distinguish between the eggs of kin and non-kin in regard to egg cannibalism (Hare & Eisner 1995). As all siblings were reared together for the first 2 wk and then apart for 2 wk prior to use in a trial, it is possible that *U. ornatrix* larvae may imprint on eggs and larvae initially and use odor as the mechanism of kin recognition. It is possible, however, that the differences between sibling and unrelated trials in our work resulted from other factors besides relatedness. Siblings were likely more similar in competitive ability than unrelated larvae due to genetic similarities or closeness in age. Even in size-matched trials, sibling larvae were more likely to be the same age than unrelated larvae because all siblings came from clusters of eggs laid by one female (females typically laid multiple egg clusters over approximately 2 wk). Larval competitive ability of other species can increase with age (Quiring & McNeil 1984). Therefore, the effect of relatedness could have been driven by differences in larval age. However, if the effect of relatedness was due to a decrease in competitive intensity between siblings or due to another factor such as larval age, our methods successfully simulated natural conditions because larvae are generally surrounded by both full siblings of the same age, due to females laying clusters of synchronously

hatching eggs, and competing, unrelated larvae. Regardless of the mechanism at work, resident larvae are more likely to maintain control around sibling larvae than unrelated larvae. Future studies should examine the ability of *U. ornatix* to recognize kin by investigating larval cannibalism based on relatedness or by testing adults for inbreeding avoidance.

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